Journal of Chemical Ecology, Vol. 22, No. 5, 1996

PINE NEEDLE OIL CAUSES AVOIDANCE BEHAVIORS IN POCKET GOPHER *Geomys bursarius*

GISELA EPPLE,[1,*] HOPE NIBLICK,[1] STANLEY LEWIS,[1] DALE L. NOLTE,[2] DAN L. CAMPBELL,[2] and J. RUSSELL MASON[3]

[1]*Monell Chemical Senses Center*
3500 Market Street, Philadelphia, Pennsylvania 19104

[2]*United States Department of Agriculture, Animal and Plant Health Inspection Service*
Animal Damage Control, Denver Wildlife Research Center
Olympia Field Station
3625 93rd Avenue, S.W., Olympia, Washington 98502

[3]*United States Department of Agriculture, Animal and Plant Health Inspection Service*
Animal Damage Control, Denver Wildlife Research Center
c/o Monell Chemical Senses Center, 3500 Market Street, Philadelphia, Pennsylvania 19104

(Received September 20, 1995; accepted January 6, 1996)

Abstract—Essential oils from coniferous trees contain secondary metabolites that act as feeding deterrents for a number of herbivorous mammals. We investigated effects of pine needle oil on feeding and other behaviors of herbivorous plains pocket gophers. In experiment 1, pocket gophers were offered sweet potato from single feeding stations placed in home cages of individually housed animals. Stations contained either a scent dispenser with pine needle oil or mineral oil. Subjects removed significantly less food from stations scented with pine needle oil. Experiment 2 was performed to investigate neophobic responses to odors. *d*-Pulegone, presented under conditions identical to those used in experiment 1, did not reduce food removal compared to mineral oil. In experiment 3 pocket gophers were observed in a maze consisting of a start box connected to two goal boxes by tunnels. One goal was scented with pine needle oil, the second with mineral oil. Subjects entered goals scented with pine needle oil significantly less frequently than goals scented with mineral oil and spent less time there. They performed all recorded behaviors at lower frequencies while located in pine-scented goals. In experiment 4 animals were introduced into a maze consisting of a start box from which two soil-packed tunnels could be entered. Embedded in the soil of one tunnel was a barrier of electrical cable that had been soaked in pine needle oil, the second tunnel contained a barrier of cable soaked in mineral oil. Pocket gophers gnawed

*To whom correspondence should be addressed.

significantly less insulation from cable treated with pine needle oil than from cable treated with mineral oil. Our results show that constituents in pine needle oil are aversive to plains pocket gophers. Under natural conditions they may function as feeding deterrents. Some of the compounds may be suitable repellents for control of pocket gopher damage.

Key Words—Pocket gophers, avoidance behavior, feeding deterrents, plant secondary metabolites, pine needle oil.

INTRODUCTION

Plants produce a great variety of secondary metabolites such as phenolics, alkaloids, and terpenoids that act as defense against herbivores (Harborne, 1991; Haslam, 1988; Langenheim, 1994). Many of these compounds are toxic, and herbivorous mammals have evolved physiological mechanisms to protect themselves from this toxicity (Freeland and Janzen, 1974; McArthur et al., 1991). They also possess behavioral mechanisms to avoid ingestion of some plants or parts of plants, and these mechanisms often are based on chemosensory detection of secondary metabolites. Snowshoe hares (*Lepus americanus*), for example, are highly selective feeders. Their avoidance of buds and catkins of Alaskan green alder (*Alnus crispa*) is mediated by two phenolic compounds, pinosylvin and pinosylvin methyl ether (Bryant et al., 1983; Clausen et al., 1986). Mixtures of phenolic secondary compounds in some structures and growth stages of balsam popular (*Populus balsamifera*) cause avoidance by the same species (Reichardt et al., 1990a). Snowshoe hares also avoid winter apical birch (*Betula* spp.) twigs containing phenolic glycosides (Iason and Palo, 1991; Sunnerheim et al., 1988), juvenile growth stages of winter-dormant paper birch (*Betula resinifera*) bearing papyriferic acid (Reichardt et al., 1984), as well as food sources with germacrone, a terpene from Labrador tea (*Ledum groenlandicum*) (Reichardt et al., 1990b).

Essential oils from conifers also contain secondary metabolites, mostly terpenoids and phenols, that act as feeding deterrents for snowshoe hare (Sinclair et al., 1988), meadow vole (*Microtus pennsylvanicus*) (Roy and Bergeron, 1990), moose (*Alces alces*) (Sunnheim-Sjoberg, 1992; Sunnheim-Sjoberg and Hamalaien, 1992), red deer (*Cervus elaphus*) (Elliott and Loudon, 1987), and mule deer (*Odocoileus hemionus columbianus*) (Schwartz et al., 1980). Industrial pine oil, a by-product of the wood pulp industry, has shown some promise as a feeding deterrent for snowshoe hare and Townsend's vole (*Microtus townsendii*) (Bell and Harestad, 1987).

Responses of pocket gophers to secondary plant metabolites have not been studied in any detail. For *Thomomys*, however, Radwan et al. (1982) showed that ponderosa pine (*Pinus ponderosa*) seedlings from some geographic areas are protected against attack, while other seedlings are heavily damaged. Different parts of the same seedling are also discriminated during feeding. Preferences are negatively correlated to stem oils, indicating that some terpenoid constituents of conifer oils are able to protect trees from gopher attacks, and therefore are potential feeding repellents.

In the present study the effects of pine needle oil and of *d*-pulegone on feeding and other behaviors of plains pocket gophers (*Geomys bursarius*) were assessed. Pocket gophers are generalist herbivores that forage mostly underground by excavating tunnels to reach food plants. These rodents cause problems by gnawing through underground cable they encounter while digging. Moreover, they are serious pests in agricultural and reforestation areas (Chase et al., 1982). Species of the genus *Thomomys*, in particular, hinder conifer reforestation by clipping roots and girdling trunks (Burton and Black, 1978; Gottfried and Patton, 1984; Radwan et al., 1982) and are also a persistent problem in orchards (Sullivan et al., 1987). Plains pocket gophers inhibit establishment of red oak (*Quercus rubra*) and white pine (*Pinus strobus*) (Huntly and Inouye, 1988) and can damage Christmas tree plantations (Hegdal, personal communication).

METHODS AND MATERIALS

Subjects. Twenty-four adult plains pocket gophers, 15 females and 9 males, served as subjects. Eighteen had been trapped near San Antonio, Texas, and six were born in the laboratory to females that were pregnant when caught. All animals were individually housed in stainless steel cages (60 × 50 cm, 22 cm high), containing aspen chips, pieces of plastic pipe (15 cm long, inner diameter 8 cm), and cardboard boxes for nesting. Purina Guinea Pig Chow, Mazur Omnivore A pellets, and a mixture of rolled oats, sunflower seeds, and peanuts were fed ad libitum and were available during all experiments. Dandelion, kale, and crab apple branches were given occasionally. The animal room was kept at approximately 21°C; light and dark phases were adjusted to reflect seasonal changes in hours of day light in Philadelphia (14L:10D in July; 10L:14D in December).

Stimulus Material. Pine needle oil was purchased from the Penn Herb Co., Philadelphia, Pennsylvania (Siberian Pine Needle Oil, catalog no. 549). A partial analysis of the oil, performed in our laboratory, showed α-pinene, β-pinene, and myrcine to be among its constituents (Wager-Pagé et al., 1996). *d*-Pulegone was obtained from International Flavors and Fragrances. Light white mineral oil NF (Lannett Co., Philadelphia, Pennsylvania) served as a control stimulus.

Experiment 1. The effect of pine needle oil on retrieval and consumption of preferred food was assessed in single-choice tests. Ten wild-born and six captive-born animals served as subjects. During each test a scented feeding station containing 10 g of diced sweet potato was placed into the subject's home cage for 1 hr. The amount of sweet potato remaining in the feeding station at the end of the trial was used as a measure of pine needle oil repellency.

Each feeding station consisted of a plastic tunnel (25 cm long, 8 cm ID) that was sealed at one end by inserting a 6-cm-deep stainless steep cup. The cup contained the sweet potato and a scent dispenser attached to the cup above the food. Tunnels were placed parallel to the front walls of the home cages and were kept from rolling by securing them with a clean brick.

Stimulus fluids (100 μl) were applied to filter paper, 3 $\times$ 9 cm, folded into 3-cm^2 pads. Papers were placed into plastic mesh capsules (HistoPrep, Fisher Scientific; 25 $\times$ 6 mm). These scent dispensers allowed the animals to smell but not to contact the stimuli and prevented contamination of the food with odorants. The volume of 100 μl resulted in a moderately strong scent that could be detected easily by the human observer at the end of the trials.

Different sets of tunnels and cups were used with mineral and pine needle oil to avoid cross-contamination. All testing equipment was machine washed at 82°C and thoroughly rinsed with clean water between trials. Scent dispensers were discarded after each trial.

Subjects were tested once with each stimulus on different days. Only eight individuals per day were tested, four receiving pine needle oil and four receiving mineral oil. The order of stimulus presentation was counterbalanced across subjects. The experiment was conducted during November. All trials were given between 14:00 and 16:00 hr. This time lies within the species' activity period under natural conditions (Benedix, 1994).

Results were evaluated in a two-factor analysis of variance (ANOVA). The independent factor was groups (two levels: wild-caught and laboratory-born individuals). The dependent factor was stimulus type (two levels: pine needle oil and mineral oil). Tukey post-hoc tests (Winer, 1962) were used to isolate differences among mean grams of food taken.

Experiment 2. To assess the possibility that responses to pine needle oil were the result of neophobia, responses to a novel odor were tested in eight wild-caught pocket gophers that had never experienced the odor and that were not included in any of the experiments with pine needle oil. *d*-Pulegone, a bird repellent (Mason, 1990) with a potent mint scent (for humans) was used. Mineral oil served as a control. The experiment was performed in July. Testing procedures were identical to those used in experiment 1. Results were evaluated by paired *t* test.

Experiment 3. The effects of pine needle oil on the behavior of pocket gophers in a maze apparatus were investigated using the 16 animals tested in experiment 1. The maze consisted of an opaque plastic start box (30 $\times$ 20 cm, 14 cm high) covered with a clear Plexiglas lid. The start box was connected to two clear plastic goal boxes (28 $\times$ 28 cm, 12 cm high) via tunnels. Each tunnel

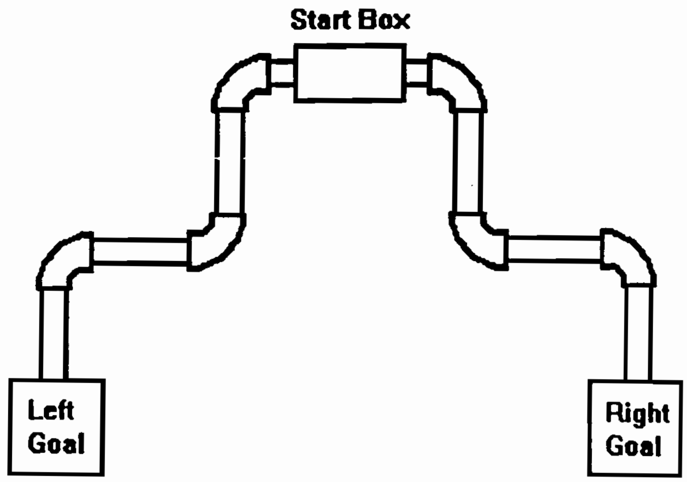

FIG. 1. The maze used in experiment 3.

consisted of three 25-cm-long secretions of translucent PVC tubing (5 cm ID) connected with 90° elbows (Figure 1). The start box was ventilated by connecting a hose attached to an opening in the lid of the box to the air exhaust of the test room.

Each goal box contained 200 ml of fresh aspen bedding and an aluminum plate (5 cm wide, 10 cm long, 4 mm thick). A HistoPrep scent dispenser containing a 3 × 9-cm strip of folded filter paper was taped to each plate to prevent the subjects from removing the dispensers from the goal box. Three cubes (2 × 2 × 2 cm) of sweet potato were placed on each plate in front of the scent dispenser.

To habituate the animals to the maze and to test for the presence of side preferences, each subject was given one trial in the clean maze, with both goal boxes containing empty scent dispensers. Following this trial, each gopher was given two trials in which the dispenser in one goal box contained 100 μl pine needle oil and the dispenser in the second goal box 100 μl mineral oil. To avoid cross-contamination, one goal box was dedicated to use with pine needle oil, the other with mineral oil. Their left–right positions were counterbalanced across subjects and replications. Between trials, equipment was washed with detergent, rinsed in water, and then soaked in 70% ethanol for several minutes.

Trials were 10 min long, divided into 60 intervals of 10 sec, indicated by an audible timer signal. At each 10-sec signal, an observer noted the location of the animal as being in the start box, the left or right tunnel system, or the left or right goal box. Behaviors were scored as Hansen frequencies (Altmann and Wagner, 1970) per 10-sec interval. For each interval the subject received a score of 1 for each of the behaviors defined below, if this pattern was displayed. The following behaviors were recorded as Hansen frequencies: (1) enter left/right goal box, (2) dig in the litter of the left/right goal box, (3) eat in left/right goal box, (4) carry food from left/right goal box, and (5) groom self in left/right goal box.

Subjects were tested between 14:00 and 16:00 hr and were only removed from their home cages when they were active. Gophers were transferred to the maze in a plastic tube and released into the start box. The 10-min trial began with the first 10-sec interval after the subject left the start box. The experiment was conducted between December and March.

For results obtained during habituation trials, differences between the subjects' location in the left and right side of the maze and between behaviors performed in these locations were compared by paired t test. Paired t tests were also used to analyze location and behavior scores recorded during experimental trials.

Experiment 4. The effects of pine needle oil on cable gnawing were investigated. Trials were performed in a maze where subjects encountered electrical cable embedded in soil. The weight of material removed from the cable in the course of an 18-hr trial was taken as a measure of the effectiveness of the pine needle oil as a repellent in this context.

The maze consisted of a linear arrangement of a start box (60 × 40 cm, 40 cm high) from which two 45-cm-long tunnels (15 cm ID) were accessible. Each tunnel was sealed at one end and completely filled with soil. It contained a barrier of three electrical cables, set in a frame and embedded in the soil 35 cm from the tunnel entry. Copper conductor cable with PVC insulation and jacket (12 mm wide, 7 mm thick) was used. The frame was made from plastic pipe (10 cm long, 12 cm ID) that fitted inside the tunnel. Three 14-cm-long pieces of cable were inserted into holes in the pipe and secured by bending them on the outside of the frame. The wires crossed each other and formed a netlike barrier that blocked the gopher's progress as it dug along the tunnel.

Twelve of the animals used in experiments 1 and 3 were each given four trials in the maze. During the first two trials, cables were untreated. During the third and fourth trials, one tunnel contained cables that had been immersed in pine needle oil for six days. The second contained cables that had soaked in mineral oil for six days. During trials with scented cable, one of the tunnels and frames was used only with pine needle oil, the other only with mineral oil. The left–right positions of the tunnels containing mineral and pine needle oils were counterbalanced across subjects and replications.

Trials were conducted overnight. Prior to each trial, the electrical cable was weighed, inserted into the frames, and embedded in fresh, commercially obtained top soil. Soaked cables were completely dried before weighing. The start box was supplied with standard diet and a small apple.

Each subject was removed from its home cage at 16:00 hr and placed into the start box of the maze. At 10:00 hr the following day, the animal was returned to its home cage. The cables were then weighed and discarded together with the used soil. Between trials, equipment was washed in a commercial cage washer at 82°C and thoroughly rinsed with clean water. Experiment 4 was performed in July and August.

Differences among weights of the material removed from the cables under unscented and scented conditions were analyzed in a two-factor ANOVA for repeated measures. Factors were conditions (two levels: clean maze and scented maze) and stimulus type (two levels: mineral oil and pine needle oil). For the latter factor, gnawing of mineral-oil-soaked wire was compared with gnawing of wire soaked in pine oil. Tukey post-hoc tests (Winer, 1962) were used to isolate differences among means.

RESULTS

Experiment 1. ANOVA revealed a significant difference between stimulus types ($F = 72.9$; 1,13 *df*; $P < 0.00001$) but no interaction between groups and stimulus types. Tukey tests showed that wild-caught as well as laboratory-born pocket gophers retrieved much less food from stations scented with pine needle oil than from stations scented with mineral oil (Figure 2).

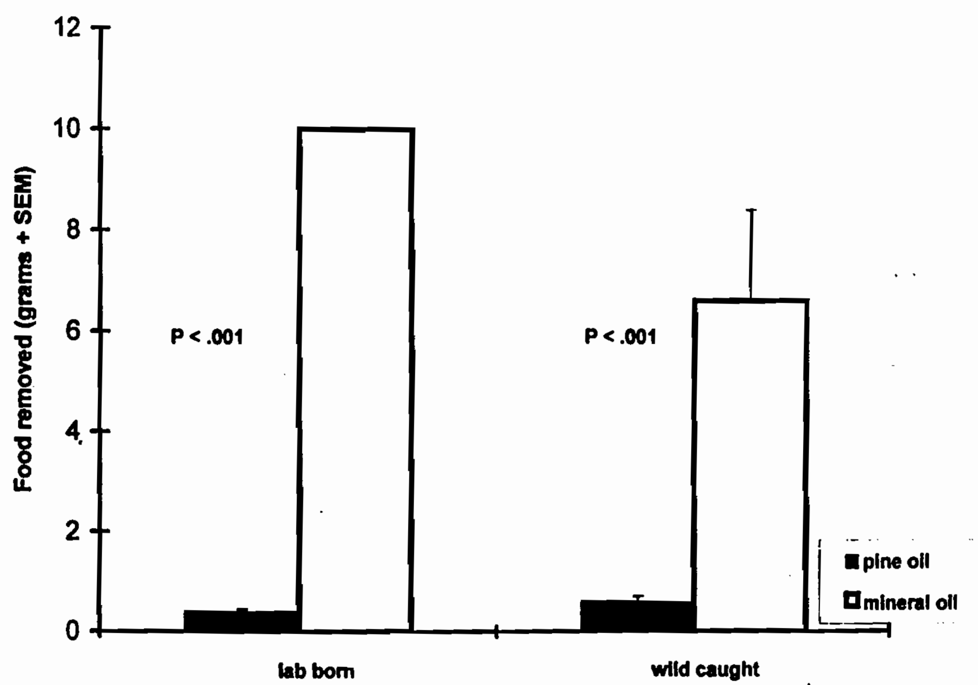

FIG. 2. Mean amount of sweet potato (SEM) removed by laboratory and wild born pocket gophers in experiment 1 from feeding stations scented with pine needle oil or mineral oil.

Experiment 2. Pulegone had no effect on food retrieval. The animals removed an average of 3.1 g (SEM 1.1 and 1.2, respectively) of food from each feeding station.

Experiment 3. The pocket gophers did not exhibit locational or behavioral side preferences during trials in the unscented maze. However, for experimental trials, *t* tests revealed significant differences between location scores in the pine needle oil scented and mineral oil scented parts of the maze and between scores for all behaviors performed in these locations (Figures 3 and 4). There were no differences in the scores obtained for being located in any of the three tunnels leading to the pine and mineral oil scented goal boxes. However, subjects entered pine needle oil scented goals significantly less frequently than mineral oil scented goals, and they were less frequently located there.

All behaviors were performed at significantly lower levels in the goal containing pine needle oil (Figure 4). Eating was particularly strongly affected, with only two of the 16 animals, one male and one female, eating while inside the pine needle oil scented goal, as compared to 12 of 16 animals eating while inside the control goal.

Experiment 4. ANOVA revealed a significant difference between stimulus types ($F = 8.0$; 1,11 *df*; $P < 0.016$) and a significant interaction between conditions and stimulus types ($F = 8.8$; 1,11 *df*; $P < 0.012$). The analysis was

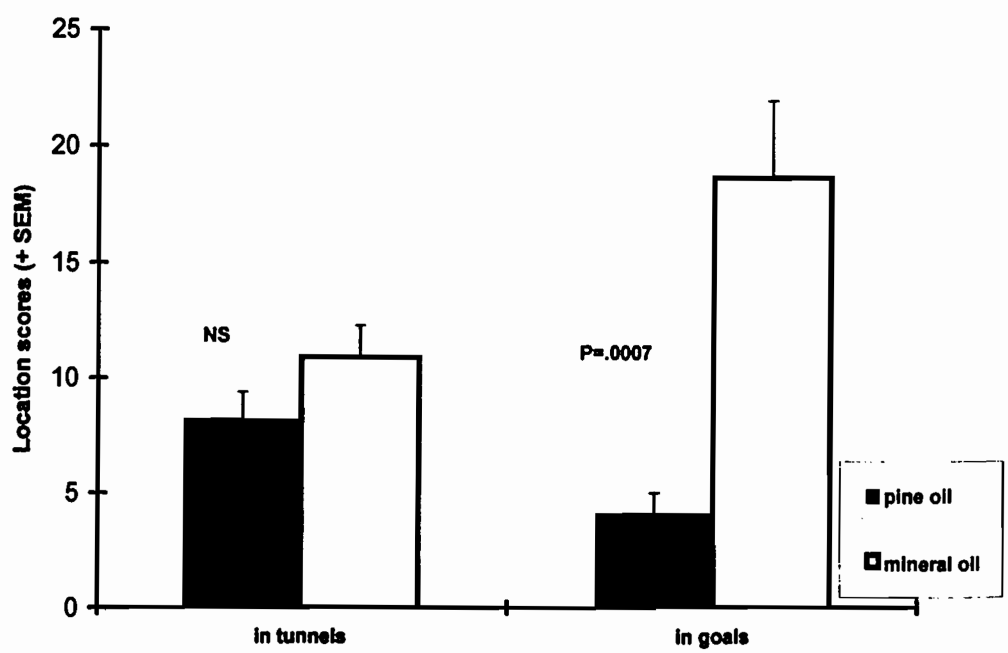

FIG. 3. Mean (+SEM) scores obtained by pocket gophers in experiment 3 for locations in tunnels leading to each goal box and in goal boxes scented with pine needle or mineral oil. NS, no significant difference.

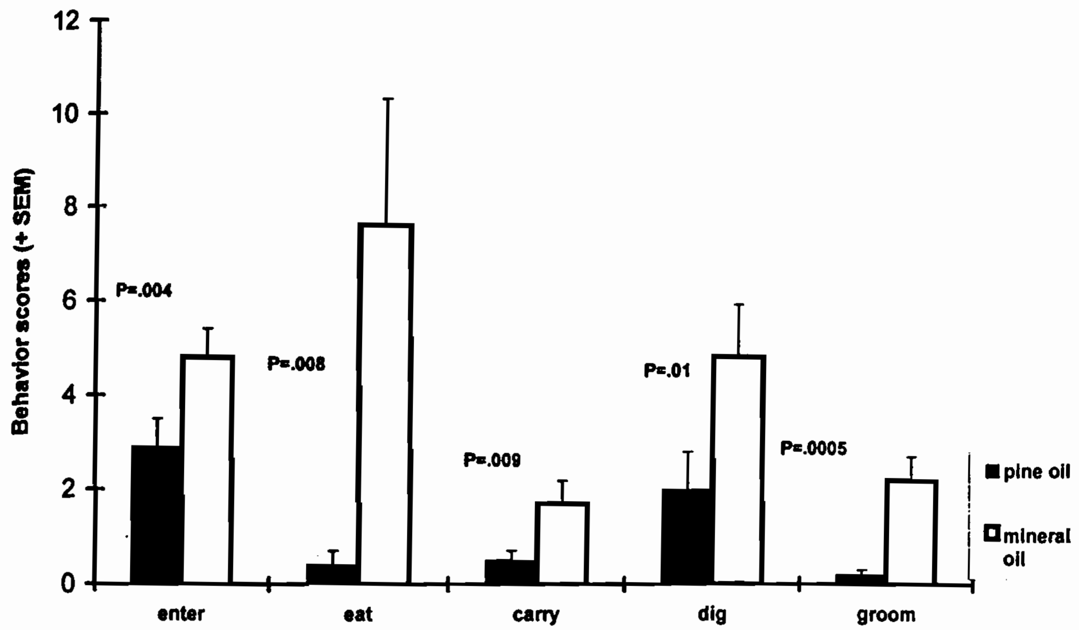

FIG. 4. Mean (+SEM) behavior scores obtained by pocket gophers in experiment 3 for entering goal boxes scented with pine needle or mineral oil and for digging, eating, carrying food, and grooming in these locations.

interpreted in terms of the interaction. During habituation trials with unscented electrical cable, no side preferences were displayed. About equal amounts of material were removed from the cables in each tunnel (Figure 5). Impregnating cable in one of the tunnels with pine needle oil did not reduce the overall amount of material removed from both tunnels, but shifted gnawing activity from pine needle oil impregnated material to that impregnated with mineral oil. Tukey tests showed that subjects removed significantly less material from wire scented with pine needle oil than that scented with mineral oil or from clean wire (Figure 5).

DISCUSSION

For the plains pocket gopher, pine needle oil is an aversive stimulus that influences behavior in a variety of contexts. Food caching was significantly reduced, as was consumption. Pine needle oil also caused area avoidance. In the maze, pocket gophers entered pine-scented chambers less frequently than chambers scented with mineral oil. All behaviors were performed less frequently in the presence of pine scent, perhaps as a result of spending less time there. Similar results were obtained in a more recent study with northern pocket gophers (*Thomomys talpoides*) that were tested in a maze comparable to that used in

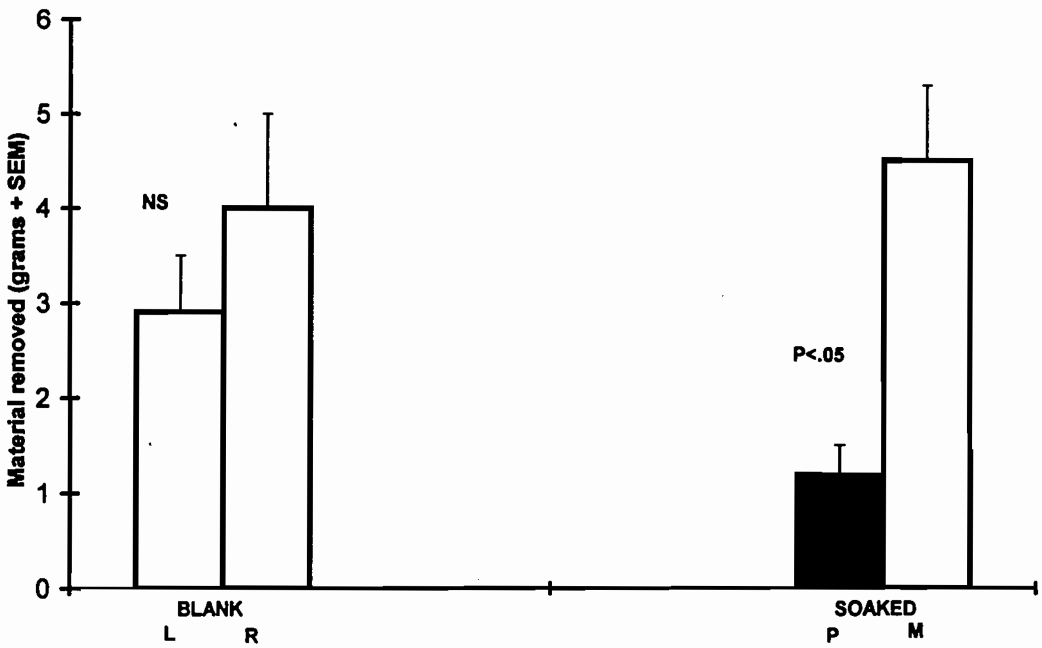

FIG. 5. Mean (+SEM) weight of material removed in experiment 4 from clean cable and from cable soaked in pine needle oil or mineral oil.

experiment 3 (Epple et al., 1996). In experiment 4, pine needle oil significantly reduced damage to soil embedded cable.

In the present study, individuals born in the laboratory and never before exposed to pine needle oil responded as strongly as wild-caught animals, about whose previous experiences with this oil or any of its components we have no information. Thus, it appears that one or several constituents of the pine oil are innately aversive to plains pocket gophers. The indifference of the animals to pulegone, a compound that is very odoriferous for the human nose, shows that this aversion is not based on neophobia. Moreover, there was no habituation to pine needle oil across experiments involving the same subjects.

In experiment 4, the pocket gophers contacted the pine needle oil soaked cable during chewing, and the stimulus could have influenced behavior via olfaction, the trigeminal system, which mediates irritation, other nasal chemosensory systems, or taste. In experiments 1 and 3, however, stimuli were enclosed in plastic capsules, and the animals could only perceive volatile cues. Although nasal trigeminal chemoreception could have been involved, the animals showed no behavioral indication of irritation, and it appears likely that avoidance was mediated, at least in part, by olfaction. Olfaction also appeared to be involved in mediating responses of northern pocket gophers to pine needle oil (Epple et al., 1996). Secondary plant metabolites are feeding deterrents for several mammalian herbivores (Iason and Palo, 1991; Langenheim, 1994; Reichardt et al., 1984, 1990a,b; Roy and Bergeron, 1990; Sinclair et al., 1988; Sunnerheim-Sjoberg and Hamalainen, 1992). Some of these species avoid deterrents on the basis of olfactory cues alone. Snowshoe hares and Townsend's voles avoid feeding from sources associated with the scent of pine oil extracted from pulp waste (Bell and Harestad, 1987). Snowshoe hares also avoid feeding on conifer seedlings to which odor dispensers with pinosylvin, a phenolic compound from Alaskan green alder (Clausen et al., 1986), have been attached (Sullivan et al., 1992). The odors of crushed foliage from lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) and of some of their monoterpene constituents inhibit feeding in red deer calves (Elliott and Loudon, 1987). Mule deer respond to the odors of juniper oil in selecting food (Schwartz et al., 1980).

The present results as well as those of our studies with northern pocket gophers (Epple et al., 1996) suggest that pine needle oil is a strong repellent for pocket gophers in general. However, the possible role the essential oil and its constituents play in controlling food selection in these species remains to be elucidated. It is likely that the animals responded to the pine needle oil because it contains compounds that act as feeding deterrents under natural conditions. Grasses constitute the most important part of the yearly diet of plains pocket gophers, although succulent forbs are preferred in spring and summer (Behrend and Tester, 1988; Benedix, 1993; Luce et al., 1980; Myers and Vaughan, 1964). Grasses and forbs do not contain essential oils, and grazers have less well-developed detoxification mechanisms than browsers and may depend more on avoidance (McArthur et al., 1991). However, plains pocket gophers consume roots of white pine and red oak (Huntly and Inouye, 1988), and under snow cover also eat above-ground parts of pine trees in Christmas tree plantations (Hegdal, personal communication). Northern pocker gophers contribute heavily to seedling mortality in fir plantations (Gottfried and Patton, 1984; Radwan et al., 1982). It is likely, therefore, that both species encounter essential oils from conifers during foraging.

Essential oils from conifers are chemically complex, being predominantly composed of monoterpene hydrocarbons (Langenheim, 1994; Radwan et al., 1982). There are differences in the composition of oils among different conifer species, different populations of the same species, individual trees, and different parts of the same plant, and animals respond to such differences (Langenheim, 1994). In the only study on pocket gophers known to us, feeding preferences of *Thomomys* (species not given) for ponderosa pine seedlings were negatively correlated to the β-pinene plus sabinene component of stem oils but positively correlated to the total terpene yield of root oils. Leaf oils, on the other hand, showed no correlation with feeding preference (Radwan et al., 1982).

In conclusion, the strong avoidance of odors from the pine needle oil used in this study suggests that compounds from this essential oil are ecologically significant for *Geomys bursarius* and might make very promising feeding repellents for other species of pocket gophers as well. Moreover, the use of pine needle oil constituents in reducing gnawing damage to underground cable should be considered. However, studies on isolation and identification of active compounds from the brand of oil used in the present experiments are needed before its use as a repellent can be explored.

Acknowledgments—The studies were supported through Cooperative Agreement Number 95-7407-0040-CA between The Denver Wildlife Research Center and The Monell Chemical Senses Center.

REFERENCES

ALTMANN, S. A., and WAGNER, S. S. 1970. Estimating rates of behavior from Hansen frequencies. *Primates* 2:181-183.

BEHREND, A. F., and TESTER, J. R. 1988. Feeding ecology of the plains pocket gopher in east central Minnesota. *Prairie Nat.* 20:99-107.

BELL, C. M., and HARESTAD, A. S. 1987. Efficacy of pine oil as repellent to wildlife. *J. Chem. Ecol.* 13:1409-1417.

BENEDIX, J. H., JR. 1993. Area-restricted search by the plains pocket gopher (*Geomys bursarius*) in tallgrass prairie habitat. *Behav. Ecol.* 4:318-324.

BENEDIX, J. H., JR. 1994. A predictable pattern of daily activity by the pocket gopher *Geomys bursarius. Anim. Behav.* 48:501-509.

BRYANT, J. P., WIELAND, G. D., REICHARDT, P. B., LEWIS, V. E., and MCCARTHY, M. C. 1983. Pinosylvin methyl ether deters snowshoe hare feeding on green alder. *Science* 222:1023-1025.

BURTON, D. H., and BLACK, H. C. 1978. Feeding habits of Mazama pocket gophers in south-central Oregon. *J. Wildl. Manage.* 42:383-390.

CHASE, J. D., HOWARD, W. E., and ROSEBERRY, J. T. 1982. Pocket gophers. Geomydae, pp. 239-255, *in* J. A. Chapman and G. A. Feldhamer (eds.). Wild Mammals of North America. The Johns Hopkins University Press, Baltimore.

CLAUSEN, T. P., REICHARDT, P. B., and BRYANT, J. P. 1986. Pinosylvin and pinosylvin methyl ether as feeding deterrents in green alder. *J. Chem. Ecol.* 12:2117-2131.

ELLIOTT, S., and LOUDON, A. 1987. Effects of monoterpene odors on food selection by red deer calves (*Cervus elaphus*). *J. Chem. Ecol.* 13:1343-1349.

EPPLE, G., NOLTE, D. L., MASON, J. R., ARONOV, E., and WAGER-PAGÉ, S. 1996. Behavioral responses to pine needle oil in the northern pocket gopher. In J. R. Mason (ed.). *Repellents Wildl. Damage Manage.* Colorado State University, In press.

FREELAND, W. J., and JANZEN, D. H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108:269-289.

GOTTFRIED, G. J., and PATTON, D. R. 1984. Pocket gopher food habits on two disturbed forest sites in central Arizona. USDA, Forst Service Research Paper RM-255. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80526.

HARBORNE, J. B. 1991. The chemical basis of plant defense, pp. 45-59, *in* R. T. Palo and C. T. Robbins (eds.). Plant Defenses Against Mammalian Herbivory. CRC Press, Boca Raton, Florida.

HASLAM, E. 1988. Plant polyphenols (syn. vegetable tannins) and chemical defense—a reappraisal. *J. Chem. Ecol.* 14:1789-1805.

HUNTLY, N., and INOUYE, R. 1988. Pocket gophers in ecosystems: Patterns and mechanisms. *BioScience* 38:786-793.

IASON, G. R., and PALO, R. T. 1991. Effects of birch phenolics on a grazing and a browsing mammal: A comparison of hares. *J. Chem. Ecol.* 17:1733–1743.

LANGENHEIM, J. H. 1994. Higher plant terpenoids: A phytocentric overview of their ecological roles. *J. Chem. Ecol.* 20:1223–1279.

LUCE, D. G., CASE, R. M., and STUBBENDIECK, J. 1980. Food habits of the plains pocket gopher on western Nebraska rangeland. *J. Range Manage.* 33:129–131.

MASON, J. R. 1990. Evaluation of *d*-pulegone as an avian repellent. *J. Wildl. Manage.* 54:130–135.

MCARTHUR, C., HAGERMAN, A. E., and ROBBINS, C. T. 1991. Physiological strategies of mammalian herbivores against plant defenses, pp. 103–114, *in* R. T. Palo and C. T. Robbins (eds.). Plant Defenses against Mammalian Herbivory, CRC Press, Boca Raton, Florida.

MYERS, G. T., and VAUGHAN, T. A. 1964. Food habits of the plains pocket gopher in eastern Colorado. *J. Mammal.* 45:588–598.

RADWAN, M. A., CROUCH, G. L., HARRINGTON, C. A., and ELLIS, W. D. 1982. Terpenes of ponderosa pine and feeding preferences by pocket gophers. *J. Chem. Ecol.* 8:241–253.

REICHARDT, P. B., BRYANT, J. P., CLAUSEN, T. P., and WIELAND, G. D. 1984. Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia* 65:58–69.

REICHARDT, P. B., BRYANT, J. P., MATTES, B. R., CLAUSEN, T. P., CHAPIN, F. S., III, and MEYER, M. 1990a. Winter chemical defense of Alaska balsam poplar against snowshoe hares. *J. Chem. Ecol.* 16:1941–1959.

REICHARDT, P. B., BRYANT, J. P., ANDERSON, B. J., PHILLIPS, D., CLAUSEN, T. P., MEYER, M., and FRISBY, K. 1990b. Germacone defends labrador tea from broswing by snowshoe hares. *J. Chem. Ecol.* 16:1961–1970.

ROY, J., and BERGERON, J.-M. 1990. Role of phenolics of coniferous trees as deterrents against debarking behavior of meadow voles (*Microtus pennsylvanicus*). *J. Chem. Ecol.* 16:801–808.

SCHWARTZ, C. C., REGELIN, W. L., and NAGY, J. G. 1980. Deer preference for juniper forage and volatile oil treated foods. *J. Wildl. Manage.* 44:114–120.

SINCLAIR, A. R. E., JOGIA, M. K., and ANDERSEN, R. J. 1988. Camphor from juvenile white spruce as an antifeedant for snowshoe hares. *J. Chem. Ecol.* 14:1505–1514.

SULLIVAN, T. P., KREBS, J. A., and KLUGE, H. A. 1987. Survey of mammal damage to tree fruit orchards in the Okanagan Valley of British Columbia. *Northwest Sci.* 61:23–31.

SULLIVAN, T. P., CRUMP, D. R., WIESER, H., and DIXON, E. A. 1992. Influence of the plant antifeedant, pinosylvin, on suppression of feeding by snowshoe hares. *J. Chem. Ecol.* 18:1151–1164.

SUNNERHEIM, K., PALO, R. T., THEANDER, O., and KNUTSSON, P. G. 1988. Chemical defense in birch. Platyphylloside, a phenol from *Betula pendula* inhibiting digestibility. *J. Chem. Ecol.* 14:549–560.

SUNNERHEIM-SJOBERG, K. 1992. (1*S*,2*R*,4*S*,5*S*)-Angelicoidenol-2-*O*-β-D-glucopyranoside—a moose deterrent compound in scots pine (*Pinus sylvestris* L.). *J. Chem. Ecol.* 18:2025–2039.

SUNNERHEIM-SJOBERG, K., and HAMALAINEN, M. 1992. Multivariate study of moose browsing in relation to phenol pattern in pine needles. *J. Chem. Ecol.* 18:659–672.

WAGER-PAGÉ, S., MASON, R., ARONOV, E., and EPPLE, G. 1996. The role of sensory cues and feeding context in the mediation of pine needle oil's repellency in prairie voles. In J. R. Mason (ed.). *Repellents Wildl. Damage Manage.* Colorado State Univ. Press, In press.

WINER, B. J. 1962. Statistical Principles in Experimental Design. McGraw-Hill, New York. 907 pp.